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Lubsch, Alexander; Timmermans, Klaas

*Published in:*  
 Botanica Marina

*DOI:*  
[10.1515/bot-2016-0075](https://doi.org/10.1515/bot-2016-0075)

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*Document Version*  
 Publisher's PDF, also known as Version of record

*Publication date:*  
 2017

[Link to publication in University of Groningen/UMCG research database](#)

*Citation for published version (APA):*

Lubsch, A., & Timmermans, K. (2017). Texture analysis of *Laminaria digitata* (Phaeophyceae) thallus reveals trade-off between tissue tensile strength and toughness along lamina. *Botanica Marina*, 60(2), 229-237. <https://doi.org/10.1515/bot-2016-0075>

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Alexander Lubsch\* and Klaas Timmermans

# Texture analysis of *Laminaria digitata* (Phaeophyceae) thallus reveals trade-off between tissue tensile strength and toughness along lamina

DOI 10.1515/bot-2016-0075

Received 20 July, 2016; accepted 21 February, 2017; online first 25 March, 2017

**Keywords:** *Laminaria digitata*; seaweed morphology; seaweed toughness; texture analysis; toughness gradient.

**Abstract:** Texture analysis is a method to test the physical properties of a material by tension and compression. The growing interest in commercialisation of seaweeds for human food has stimulated research into the physical properties of seaweed tissue. These are important parameters for the survival of sessile organisms consistently exposed to turbulent flow and varying drag-forces. These tactile properties also affect consumer perception and acceptance of materials. Here, we present a standardised method to determine these physical properties using, as an example, the brown seaweed *Laminaria digitata* (Hudson) J.V. Lamouroux, which is prevalent on coastlines along the northern Atlantic Ocean. Morphological features of a healthy *L. digitata* thallus (lamina) seem modified to withstand physical distress from hydrodynamic forces in its wave-swept habitat. The trade-off in tissue responses to tensile and compression forces along the lamina, linked to an age gradient, indicates a twinned alignment of its cellular microstructure, similar to those of modern nanotechnology, to optimise the toughness and flexibility of constituent tissue. Tensile strength increased from young to old tissue along a positive toughness gradient of 75%. Based on our results, a short interpretation is given of the heterogeneity in *L. digitata* lamina from morphological, ecological and physiological perspectives.

## Introduction

Texture analysis is a method used to test the physical properties of a material by applying tension and compression. These parameters allow for calculation of multiple properties, such as resilience, hardness, breaking-point, firmness and spreadability, depending on the physical state of the materials, ranging from fluid to solid. Texture analysis has been commonly used in the food industry since the early 1960s to evaluate and standardise the tactile properties of food products (Szczesniak 1963), as such information affects consumer perception and acceptance of materials, in addition to their visual assessment (e.g. Szczesniak and Kleyn 1963, Peck and Childers 2003). Texture analysis has been used on conventional foods, ranging from baked goods, like biscuits, to raw fruits, like watermelons.

Edible seaweeds are on the verge of entering the commercial market for human food in the Western hemisphere, and the general demand for seaweed products has been increasing globally during the last decade. This has stimulated efforts towards (mass) cultivation in addition to wild harvesting (e.g. Neori 2008, Bixler and Porse 2011, Holdt and Kraan 2011, Kraan 2013). Only limited standardised data exist on the physical properties of seaweeds. However, these are important parameters for the selection and survival of these sessile organisms, which are consistently exposed to turbulent flow and its varying drag-forces during their development. Water velocities can be as high as  $14 \text{ m s}^{-1}$  and can result in strong hydrodynamic forces on intertidal and shallow subtidal marine plants, like seaweed (e.g. Koehl 1984, Denny 1994). Knowledge about morphological and physical properties can also be important for selecting and adjusting pre-treatments to process raw material prior to bio-refining processes (Zhu and Pan 2010). Yet information on morphology and

**\*Corresponding author: Alexander Lubsch**, Department of Estuarine and Delta Systems, NIOZ Royal Netherlands Institute of Sea Research, and Utrecht University, PO Box 140, 4401 NY Yerseke, The Netherlands; and Department Ocean Ecosystems, University of Groningen, PO Box 72, 9700 AB Groningen, The Netherlands, e-mail: alexander.lubsch@nioz.nl

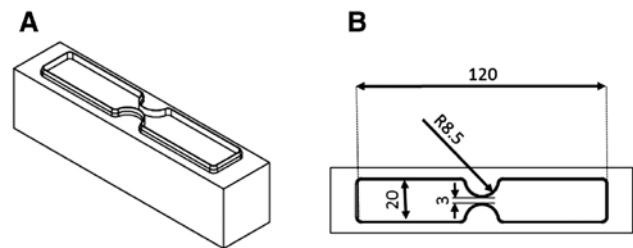
**Klaas Timmermans:** Department of Estuarine and Delta Systems, NIOZ Royal Netherlands Institute of Sea Research, and Utrecht University, PO Box 140, 4401 NY Yerseke, The Netherlands; and Department Ocean Ecosystems, University of Groningen, PO Box 72, 9700 AB Groningen, The Netherlands

physical properties, such as the strength and toughness of seaweed, appears to be fragmented and dispersed (Thomsen and Wernberg 2005).

The hydrodynamic environment influences the morphology and biomechanics of seaweeds. For example, hydrodynamic drag can be related to the effects of diffusion boundary layers (DBL). As the thickness of the DBL decreases with increasing hydrodynamic forces, drag has an impact on the acquisition of essential resources (Hurd 2000). Another example is the relationship between tensile strength and physical dislodgement by waves. A small number of studies have investigated the tensile strength of different seaweeds *in situ* by using a spring scale to apply pull-tests horizontally to the substratum until the seaweeds were dislodged (Jones and Demetropoulos 1968, Carrington 1990, Hawes and Smith 1995, Bell 1999). As dislodgement of seaweeds is a major factor in determining their survival and distribution (Norton 1991, Denny 1995), knowledge about the physical properties that affect dislodgement can help us to understand how population dynamics and community organisation could develop in response to more extreme weather patterns (Berg and Ellers 2010, Young et al. 2011, Coumou and Rahmsdorf 2012).

During storms, seaweeds do not necessarily break off at the stipe (Carrington 1990, Shaughnessy et al. 1996, Milligan and DeWreede 2000), and thallus morphology has been suggested to be the central factor mitigating these break forces (Denny 1995, Boller and Carrington 2006). Thallus damage, such as that caused by herbivores, can lead to extended rupture and loss of distal tissue (Koehl and Wainwright 1977, Santelices et al. 1980, Munoz and Santelices 1989). Herbivore-like damage is commonly measured by puncturing or compressing the tissue, either with a gravitational penetrometer or an industrial texture analyser. The physiological resistance to compression is termed (tissue) toughness and has only been examined in a few ecological studies on changes in the phenotypic plasticity of seaweed as a response to biotic and abiotic stress (e.g. Lowell et al. 1991, Pratt and Johnson 2002, Toth and Pavia 2007, Molis et al. 2015).

In this study we present, for the first time, a standardised texture analysis of tissue strength and toughness along the central lamina of the thallus in cultivated *Laminaria digitata* (Hudson) J.V. Lamouroux. We introduce a methodology to determine breaking points by means tensile and compression forces, as well as total strain deformation ( $\epsilon$ ) using an industrial texture analyser mounted with customised clamps for attaching samples.



**Figure 1:** Technical drawing of press block from different angles (A, B). (A) Sketch of press block used to punch out tissue samples for measuring ultimate tensile strength (UTS) in diagonal view. (B) Schematic top view of the press block, including dimensions (mm).

## Materials and methods

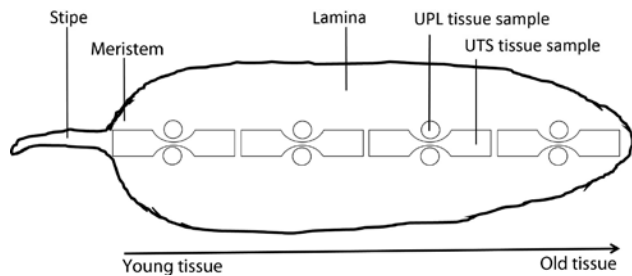
### Experimental set-up

A cohort of 1-year-old individuals of *Laminaria digitata* were obtained from cultivation tanks at the NIOZ (Royal Netherlands Institute for Sea Research) seaweed centre ([www.nioz.nl/seaweedcentre](http://www.nioz.nl/seaweedcentre)) in April 2015. They were kept in a cool box (15 l) filled with ambient seawater (14°C, salinity 29.3) during analysis in the laboratory. Individuals ranged from 36 to 68 cm in length, based on measurements of the central lamina of the thallus from stipe to tip, and showed no physical damage nor epiphytes.

A custom built press block (Figure 1) was used to punch out pieces of tissue (120×20 mm) with two wings and a narrow central section of 3 mm to test the ultimate tensile strength (UTS) of the tissue, which measures the pulling force necessary for tissue rupture. In addition, disc-shaped samples were also punched out, using a polyethylene vial ( $\varnothing=11$  mm) as a perforator, to test the ultimate piercing load (UPL), which is the load needed to pierce through tissue and is used to measure tissue toughness.

All punched-out material was taken from the central lamina in a repetitive pattern along the tissue age gradient from stipe to tip (Figure 2). Young tissue develops from the meristem located at the base near the stipe in *L. digitata*, which results in the oldest tissue being located at the tip or apex. Three to four tissue samples for UTS and UPL measurements were punched out along the central lamina (Figure 2), and the relative distances of punched out samples from the stipe were determined for each individual ( $n=11$ ).

Tissue thickness around the narrow centre of the stamp was measured in two places with a digital vernier calliper (accuracy  $\pm 0.1$  mm) and averaged for data treatment. Analysis of UTS and UPL as measurements of responses to tension and compression were conducted with a texture analyser (CT3, Brookfield Engineering, USA;

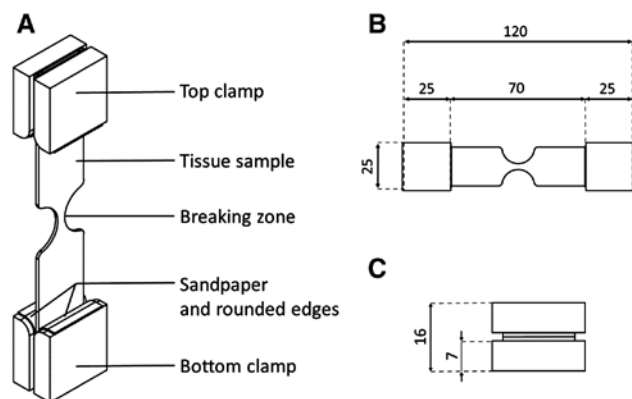


**Figure 2:** Sketch of lamina of *Laminaria digitata* (1-year-old) including pattern of tissue samples punched-out for measuring ultimate tensile strength (UTS) and ultimate piercing load (UPL) along the central axis and age gradient.

Young tissue develops from the meristem, resulting in oldest tissue at the apical tip.

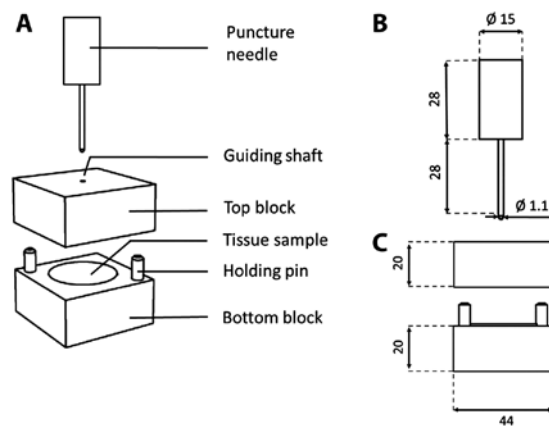
kindly provided by the Department of Aquatic Biotechnology and Bioproduct Engineering, Faculty Mathematics and Natural Sciences, University of Groningen), equipped with a 1000 g load cell. Custom-built clamps (Figure 3) and mounts (Figure 4) to hold the sample in place during measurements were built at the NIOZ workshop. All customised items attached to the analyser were weighed and a corresponding pre-programmed “trigger load” (2 g) was chosen (Brookfield TexturePro CT software package, firmware version 2.1, Brookfield Engineering, USA). The test speed in both measurements, tension and compression, was set to a constant velocity of  $0.2 \text{ mm s}^{-1}$ .

Measuring UTS required the double-winged tissue sample to be evenly fixed with each end attached to a top and bottom clamp (Figure 3A–C), which were rigidly attached



**Figure 3:** Technical drawing of attachment clamps and attached sample from different angles (A–C).

(A) Sketch of set up to analyse ultimate tensile strength (UTS). The tissue sample is fixed between the top and bottom clamps (attached to the texture analyser). The clamps have rounded edges to avoid damage and a layer of sandpaper prevents the sample from slipping during UTS analysis. (B) Front view and dimensions (mm) of the set up with clamps. (C) Top view and dimensions (mm) of a clamp (round edges not illustrated).



**Figure 4:** Technical drawing of fixation block and puncture needle from different angles (A, B).

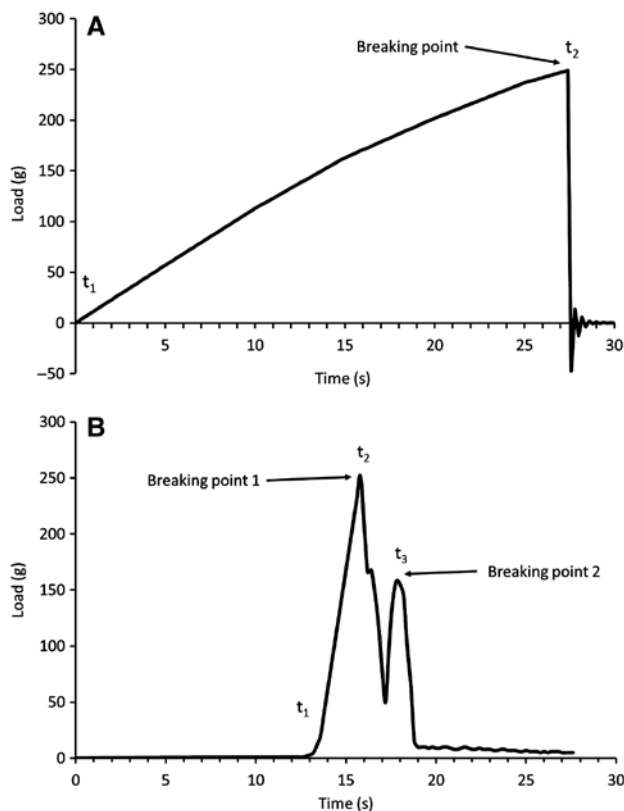
(A) Sketch of set up to analyse ultimate piercing load (UPL). The tissue sample is fixed between the top and bottom blocks. A shaft ( $\text{Ø } 1.2 \text{ mm}$ ) guides a puncturing needle through both blocks, which are held in alignment by pins at the bottom and corresponding holes drilled into the top block. The puncturing needle is attached to the texture analyser. (B) Side view and dimensions (mm) of the puncturing needle. (C) Side view and dimensions (mm) of the top and bottom blocks (guiding shaft is not illustrated).

to the beams of the texture analyser. Each clamp consisted of two solid aluminium plates ( $25 \times 25 \times 7 \text{ mm}$ ) facing each other (Figure 3B and C). Rounded edges ( $90^\circ$ ) and a layer of sandpaper (P100) on the inner sides of the plates prevented the fixed wet sample from either edge effects or slippage when subjected to tension forces, and ensured an accurate replication of UTS with the narrow centre of the sample as the pre-determined breaking zone (Figure 3A).

For UPL analysis, a disc-shaped tissue sample was placed between two solid PVC blocks ( $44 \times 44 \times 20 \text{ mm}$ ) with a guiding shaft ( $\text{Ø} = 1.2 \text{ mm}$ ) for the puncture needle ( $\text{Ø} = 1.1 \text{ mm}$ ) at the centre (Figure 4A–C). Two holding pins on the bottom block (and corresponding holes drilled into the top block) guaranteed an exact alignment of the superimposed guiding shafts of each block and, hence, a “barrier-free” slide for the stainless steel puncture needle with a plain tip. To minimise friction in the shaft, the needle was liberally coated with a lubricant (Vaseline).

## Data treatment

Typical graphs of UTS and UPL measurements on *Laminaria digitata* are illustrated in Figure 5A and B. During UTS measurement, the sample is exposed to a linear increase in length from time  $t_1$ , resulting in an increased pulling force until it snaps at time  $t_2$ . The UTS represents the maximum applied force (load) before the tissue snaps (Figure 5A) and



**Figure 5:** Example graphs of texture analysis of *Laminaria digitata*. Typical graphs of tension (A) and compression (B) measurements during texture analysis of *Laminaria digitata* samples. Measurement starts at time  $t_1$ . (A) The breaking point at  $t_2$  indicates rupture of the sample, referred to as ultimate tensile strength (UTS) of the tissue. (B) Breaking point 1 at  $t_2$  indicates rupture of the external cell wall by the puncturing needle, which indicates ultimate piercing load (UPL). Breaking point 2 at  $t_3$  represents the internally initiated rupture of the cell wall on the opposite side.

the data obtained were normalised to the cross-sectional area of the narrow breaking point:

$$UTS = \frac{F_m}{w \cdot d}$$

where  $F_m$  = recorded load (g),  $w$  = width of the sample at breaking point (3 mm, Figure 3B) and  $d$  = thickness of the sample (mm).

Before the UTS was reached, the tissue sample was stretched linearly by pulling forces (Figure 5A) and the resulting relative strain deformation ( $\epsilon_t$ ) was calculated:

$$\epsilon_t = \frac{L_t}{(t_2 - t_1) \cdot v_{tx}}$$

where  $L_t$  = Length of the tested area (70 mm, Figure 3B),  $t_1$  = starting time of applied force,  $t_2$  = time of tissue rupture, and  $v_{tx}$  = test velocity of texture analyser (0.2 mm s<sup>-1</sup>).

In contrast, UPL analysis shows two breaking points (Figure 5B). The breaking point at  $t_2$  represents the maximum applied load before the external side of the cell wall collapses (UPL), and  $t_3$  depicts the internal disruption of the cell wall on the opposite side. The UPL measurements were expressed relative to surface area (mm<sup>2</sup>):

$$UPL = \frac{F_m}{\pi \cdot r^2}$$

where  $F_m$  = recorded load (g) and  $r$  = radius of the plain tip of the puncture needle (0.55 mm, Figure 4B). The internally initiated breaking of the cell wall at  $t_3$  was disregarded in the calculations.

## Statistics

All data were tested for normality using the Kolmogorov-Smirnov test (KS test) for cumulative probability distribution. A one-way repeated measures ANOVA was performed to test for significant differences between tissue thickness,  $\epsilon_t$  and UTS, as well as for differences in UPL between all individuals and within each lamina at different relative distances from the stipe. Statistical comparison of thallus variables at successive relative distances from the stipe within individuals was conducted with paired t-tests. Significance level in all analyses was set at  $\leq 0.05$ .

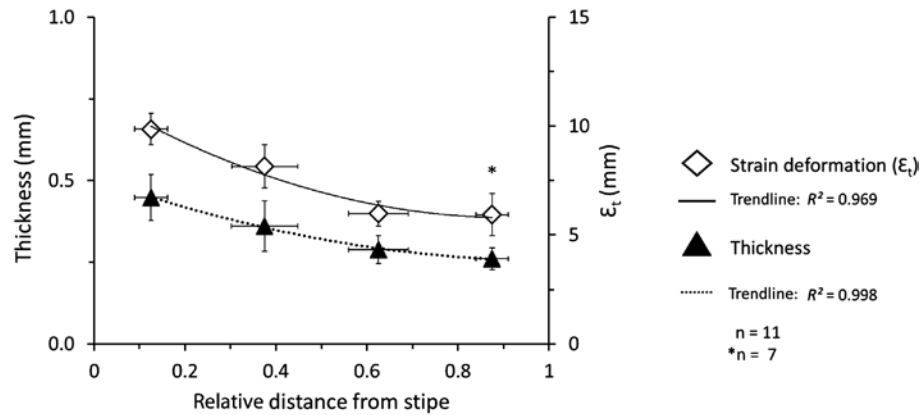
## Results

Lamina thickness did not differ significantly among individuals (groups), but there was a highly significant difference in thickness within a lamina (Table 1). Tissue

**Table 1:** One-way repeated measures ANOVA of thallus thickness, relative strain deformation ( $\epsilon_t$ ), ultimate tensile strength (UTS) and ultimate piercing load (UPL) among individuals (groups) and within the lamina of *Laminaria digitata*.

Parameter	df	F	p-Value
Thickness			
Group	10	1.10	0.396
Lamina	3	3.92	0.006
$\epsilon_t$			
Group	10	0.76	0.529
Lamina	3	0.69	0.656
UTS			
Group	10	0.45	0.907
Lamina	3	8.83	<0.001
UPL			
Group	10	3.11	0.078
Lamina	3	12.49	<0.001





**Figure 6:** Mean strain deformation ( $\epsilon_t$  in mm) and tissue thickness (mm) of *Laminaria digitata* samples at different relative distances from the stipe.

Error bars are standard deviations ( $n=11$  for tissue thickness,  $n=7$  for distance).

thickness was negatively correlated with distance from the stipe ( $R=-0.968$ ), with thickness decreasing from the stipe ( $0.45 \pm 0.07$  mm) to the tip ( $0.26 \pm 0.03$  mm) of each lamina, which amounts to a 40% reduction in thickness (Figure 6). Thus tissues became thinner with age.

Tissue thickness showed a positive correlation ( $R=0.698$ ) with the strain deformation ( $\epsilon$ ) that was observed during exposure to pulling forces. The mean  $\epsilon$  for all tested tissue samples before rupture was  $7.54 \pm 1.45$  mm, resulting in a relative strain deformation ( $\epsilon_t$ ) of  $11 \pm 2\%$ . No significant differences were found in  $\epsilon_t$  among individuals or within a lamina (Tables 1 and 2).

For UTS, no significant differences were found among individuals, but highly significant differences were found within the lamina (Table 1). There was a positive correlation ( $R=0.701$ ) of UTS with the relative distance from the stipe, and hence with the age of the tissue. Young tissue, which comprised  $12.5 \pm 3.6\%$  of the lamina length from the stipe, showed a mean UTS of  $246 \pm 36$  g mm $^{-2}$ , which was significantly weaker than tissue located  $37.5 \pm 7.3\%$  from

the stipe with a mean UTS of  $389 \pm 52$  g mm $^{-2}$  (Figure 7). The highest pulling forces necessary for tissue rupture were measured at approximately two-thirds ( $62.5 \pm 6.6\%$ ) of the lamina length from the stipe with a mean load of  $429 \pm 76$  g mm $^{-2}$ , which was 74.5% stronger than the mean UTS of young tissue (Figure 7).

Like UTS, UPL showed no significant differences among individuals but showed highly significant differences within the lamina (Table 1). In contrast to UTS, however, no correlation ( $R=-0.188$ ) was found between UPL and relative distance from the stipe. Young tissue at  $12.5 \pm 3.6\%$  of the lamina length had a mean UPL of  $327 \pm 71$  g mm $^{-2}$  and was significantly less tough than tissue found at around one third of the lamina's length (Table 2) with a mean UPL of  $432 \pm 80$  g mm $^{-2}$  (Figure 7), which was the highest UPL measured along the lamina. A continuous and significant decrease in UPL to  $292 \pm 39$  g mm $^{-2}$  in the oldest tissue resulted in an UPL gradient of 32.3% along the lamina length (Figure 7).

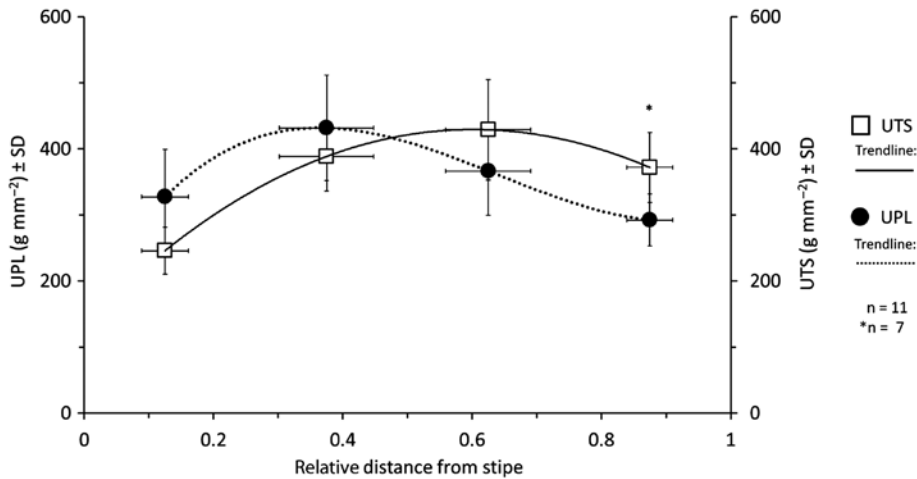
## Discussion

This study proposes a standardised method to examine, for example, the effects of hydrodynamic forces on seaweed individuals, as well as providing data on between-individual and within-lamina heterogeneity in tissue strength and toughness of *Laminaria digitata* lamina. Based on our measurements, we give a short morphological, ecological and physiological interpretation of tissue strength and toughness as a fundamental physical adaptation for survival in wave-exposed habitats. In addition, design options for artificial structures to support seaweed during cultivation are discussed.

**Table 2:** Results (p-values) from paired t-tests ( $n=11$ ) assessing differences in thallus thickness, relative strain deformation ( $\epsilon_t$ ), ultimate tensile strength (UTS) and ultimate piercing load (UPL) within the central lamina of *Laminaria digitata* at successive relative distances from the stipe (in %).

Parameter	Distance from stipe (%)			
	12.5±3.6	37.5±7.3	62.5±6.6	87.5±3.6
Thickness	0.080	0.021	0.050	
$\epsilon_t$	0.819	0.286	0.383	
UTS	<0.001	0.061	0.014	
UPL	0.021	0.043	0.005	

Distances from stipe are means  $\pm$  standard deviation ( $n=7$ ).



**Figure 7:** Mean ultimate tensile strength (UTS) and ultimate piercing load (UPL) of the central lamina of *Laminaria digitata* at different relative distances from the stipe.

Error bars are standard deviations ( $n = 11$  for tissue thickness,  $n = 7$  for distance).

## Morphology

In the intertidal and subtidal zones, which encompass the habitats for all seaweeds, water currents change their direction frequently; thus, seaweed toughness and flexibility are key factors for them to endure mechanical stress caused by hydrodynamic forces. As drag forces are a function of the surface area of seaweed (Carrington 1990), drag values will change as the seaweed grows over time (Denny et al. 1985, Denny and Gaylord 2002).

Different strategies are used by different seaweeds to effectively counter the impact of kinetic energy ( $E_k$ ) on the load-bearing stipe and the rooting holdfast in order to prevent breakage or detachment from the substrate. The strategies of hydrodynamic streamlining, with narrower and flatter blades, as well as the development of elongated cells have been reported for *Saccharina latissima* (Linnaeus) when subjected to constant longitudinal drag compared with individuals grown without stress (Gerard 1987). Elongation of cells reduces the relative (residual) biomass found towards the apex of the lamina. This biomass reduction, in turn, reduces the movement acceleration of the lamina in the opposite direction by transferring kinetic energy ( $E_k$ ) along the lamina to an increasing residual mass, which helps to mitigate the impacts of  $E_k$  on the critical attachment areas of the stipe and holdfast. In our study, a similar morphological characteristic is represented by the decrease in tissue thickness of *Laminaria digitata* lamina along an age gradient from newly formed, young tissue near the meristem to old tissue at the apex (Figure 6). This decrease in thickness can be linked to the elongated growth of cells as they age, rather than the abrasion of outer cell layers increasing towards the apex.

This is supported by the relatively uniform strain deformation ( $\epsilon$ ) of  $11 \pm 2\%$ , which showed no significant variation along the lamina (Table 1) before the sample broke during UTS measurements.

Adaptations of morphological and mechanical properties in seaweeds include modification of the microstructural composition of the cells, such as incorporation of cellulose, the structure of alginate blocks, or the packing density of cells (Mackie and Preston 1974, LaBarbera 1985, Koehl 1986). As the alignment, structure, composition and density of cells influence the mechanical properties and their feedback to tensile and compressive forces, these aspects can be linked to the alternating dominance of UTS (highest closer to apex) and UPL (highest closer to meristem) along the lamina and along an age gradient (Figure 7). UTS and UPL alternated within the same range of values, and the minimum and maximum values were not significantly different from each other, with UPL being 23% higher than UTS in young tissue and UTS being 23% higher than UPL in old tissue.

A microstructural modification to increase UTS becomes apparent in the apical third of the lamina, where UTS nearly doubled and reached maximum values, while UPL continued to decrease until it reached the same values as in young tissue (Figure 7). This significant decline in UTS around the apex (Table 2) can be explained by the decreasing necessity to support distal portions of tissue. This modification follows over time, as no significant variations in UTS and UPL values at relative distances from the stipe were observed among individuals (Table 1). The reciprocity in dominance of UTS and UPL within the lamina suggests a twinned alignment of its cellular microstructure.

The ability of twinned alignments to improve strength and toughness can be found in historical manufacturing

processes of ropes and in modern nanotechnology. For example, Liu et al. (2009) pointed out that tensile strength of nanotube yarns depend not only on the diameter but also on the twisting angle of the yarn.

## Tissue toughness, ecology and herbivory

Seaweed morphology also serves as a mechanical defence against herbivores (Mauricio 1998), and tissue toughness is the first physical barrier to overcome herbivores. UPL describes the force that mandible-bearing mesograzers, such as amphipods and isopods, have to apply in order to “bite” and feed on pieces of seaweed tissue. According to optimal defence theory (ODT; after Rhoades 1979), the parts of a seaweed that have a great ecological value to the plant are protected more intensively than other parts. Additionally, many seaweeds may combine several types of defences without paying considerable trade-off costs (Koricheva et al. 2004). As the meristem represents tissue of great ecological value, the tough texture of young tissue near the meristem in *Laminaria digitata* appears to reflect morphological protection in accordance with ODT. The 40% greater thickness of young tissue, near the meristem within the basal third of the lamina, compared with the apical third (Figure 6) impedes initial mesograzers access to young tissue. This higher thickness in the basal third of the lamina is linked with a 32% increase in tissue toughness, as measured by UPL, and herbivores would have to increase their grazing efforts to bite into this tissue. Morphological modifications and chemical defences in the responses of seaweeds to biotically and abiotically mediated stress and their ecological effects have been well documented in some species (e.g. Agrawal 2001, Toth and Pavia 2007, Utsumi 2011, Molis et al. 2015). For example, tissue toughness in *Fucus vesiculosus* was shown to exhibit plasticity to the prevailing level of wave exposure, which in turn affected the phenotypic plasticity of the radula in the grazing flat periwinkle, *Littorina obtusata* (Molis et al. 2015). However, in wave-swept, rocky coastlines with high water velocities, the accessibility of seaweed to small grazers is restricted to periods of weak hydrodynamic impact. Thus, it can be assumed that the morphological features of healthy *L. digitata* lamina are more influenced by physical distress from hydrodynamic forces than defence against herbivory.

## Physiology and cultivation practices

Seaweed morphology can be affected by hydrodynamics, but the morphology also affects the hydrodynamics

around the seaweed, which influences physiological processes like nutrient uptake. Seaweeds can actively engineer their own microhabitats through morphological features, like hydrodynamic streamlining, hyaline hairs, small corrugations and edge undulations, that affect the water velocities above the surface of the thallus, create turbulence and have an influence on the thickness of the DBL. These processes, in turn, can help to facilitate resource (nutrient) supply (Hurd et al. 1993, Hurd 2000, Hurd and Pilditch 2011). These aspects are not only important for the physiology of seaweeds but also very relevant for the design of artificial seaweed-supporting structures. The set-up for seaweed cultivation should be optimised for nutrient availability, considering both structural support elements as well as the scale of cultivation. For example, when seaweed is cultivated for carbohydrates, a flexible cultivation set-up should allow for multiple hydrodynamic forcing on a flexible seaweed so that the seaweed invests in structural elements of the cell wall, increasing carbon content. More knowledge about the phenotypic plasticity and physical trade-off between UPL and UTS, also on a cellular level, is necessary not only to understand and develop tools to modify mechanical properties in mariculture applications, but also to understand the morphological, ecological and physiological responses of seaweeds and seaweed communities to changing environmental conditions, such as under global climate change.

The approach presented in this study, using the example of *Laminaria digitata*, allows for quantification of mechanical stress resistance and may be applicable to population biology, cultivation purposes, pre-treatment before bio-refinery, and consumer perception and acceptance of a novel food. Seaweeds are becoming more and more popular as a food source for humans in Europe, the “new grazers”. Our standardised method offers opportunities to quantify tissue toughness in different parts of seaweeds, enabling selection of the most favourable parts to be consumed. It also allows for standardised methods of determining the effects of varying hydrodynamic forces and nutrient availability on seaweed.

**Acknowledgements:** We would like to thank to Prof. Dr. Marc van der Maarel and Alle van Wijk (Faculty of Mathematics and Natural Sciences, Department of Aquatic Biotechnology and Bioproduct Engineering, University of Groningen, The Netherlands) for making the texture analyser available. We also thank the NIOZ workshop, Edwin Keijser, Roel Bakker and Johan van Heerwaarden for their efforts, technical drawings and development of seaweed mountings and fittings to the texture analyser. The work



and assistance in the laboratory by Mick Peerdeman and Willem Rennes is greatly appreciated.

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sustainable seaweed farming in the North Sea area and he is particularly interested in seaweed ecology, cultivation and its biotechnological applications.

**Klaas Timmermans**

Department of Estuarine and Delta Systems, NIOZ Royal Netherlands Institute of Sea Research, and Utrecht University, PO Box 140, 4401 NY Yerseke, The Netherlands; Department Ocean Ecosystems, University of Groningen, PO Box 72, 9700 AB Groningen, The Netherlands

Klaas Timmermans is a senior scientist at NIOZ Royal Netherlands Institute for Sea Research, Department of Estuarine and Delta Systems, and Utrecht University, The Netherlands and an honorary Professor of Marine Plant Biomass at Groningen University, The Netherlands. His research interests are in ecophysiology and ecology of seaweeds.

## Bionotes

**Alexander Lubsch**

Department of Estuarine and Delta Systems, NIOZ Royal Netherlands Institute of Sea Research, and Utrecht University, PO Box 140, 4401 NY Yerseke, The Netherlands; and Department Ocean Ecosystems, University of Groningen, PO Box 72, 9700 AB Groningen, The Netherlands

[alexander.lubsch@nioz.nl](mailto:alexander.lubsch@nioz.nl)

Alexander Lubsch obtained his MSc in Marine Science from the University of Rostock (Germany) in collaboration with Alfred Wegener Institute (AWI, Helgoland, Germany), where he worked on the differential palatability of floating and non-floating seaweed parts by meso-grazer. Currently, he is a PhD candidate at the Royal Netherlands Institute for Sea Research (NIOZ), Department of Estuarine and Delta Systems, and Utrecht University, The Netherlands. His doctoral research is on the feasibility of